51. Polychæta from the N.E. Pacific : The Chætopteridæ. With an Account of the Phenomenon of Asexual Reproduction in *Phyllochætopterus* and the Description of Two new Species of Chætopteridæ from the Atlantic.

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(Plates I.–VI.† and Text-figures 1–13.)

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Introduction.

The Chætopterids found in the coastal waters of the Gulf of Georgia and Puget Sound, though the species are few in number, are very widely distributed and remarkably interesting in their biology and morphology. My observations were made on three species, all of which appear to be new :—

Mesochætopterus taylori, gen. et sp. n.
Phyllochætopterus prolifica, sp. n.
Telepsavus sp.

Of these *Mesochætopterus* partly bridges the gap between the remarkable form *Chætopterus* and the other members of the family. *Phyllochætopterus prolifica* possesses a type of asexual reproduction which is now described for the first time in the Polychæta‡. *Telepsavus* is a genus hitherto only known

* Communicated by the Secretary.
† For explanation of the Plates see p. 993.
‡ A preliminary note on this phenomenon was published in Rep. Brit. Assoc. Adv. Science, 1912, Dundee, p. 513.

to occur in the Mediterranean and the Red Sea. In previous collections the Chætopterids appear to have been represented only by empty tubes, and their interest has remained unsuspected (*cf.* Johnson, "The Polychæta of the Puget Sound Region," Proc. Boston Soc. Nat. Hist. vol. xxix. p. 386).

The collections, of which the worms described here form a part, were made in the summer of 1911, while I was a guest at the Biological Laboratory at Departure Bay, Vancouver Island, which is maintained by the Dominion Government. I should like to express my heartiest thanks for the hospitality extended to me there. The tidings of the death of the Rev. G. W. Taylor, the first Director of the Station, reached me here last year (1912), and I wish to place on record some slight tribute to the memory of one of the pioneers of marine biology in British Columbia. His enthusiasm for the study of the rich fauna of the Pacific Coast, and the patient care which he bestowed upon its investigation are worthy of great praise. I only knew him in the last year of his life, during a time when, crippled by paralysis, he suffered greatly, but his kindness and thoughtfulness will always remain a pleasant memory to me.

In connection with my work in Canada, I wish, too, to gratefully acknowledge my indebtedness to the Managers of the Balfour Fund, who made me a special grant to assist in defraying the expenses of the journey.

Of the other forms which are described in this paper, *Mesochætopterus minuta* was found amongst the collection made by Mr. Cyril Crossland in the Cape Verde Islands during July and August 1904. I am much obliged to him for permission to describe this form, and for his kindness in reading through this paper. Lastly, the new species of *Phyllochætopterus*, which I have found to be an inhabitant of British waters, was obtained while working at the Laboratory of the Marine Biological Association at Plymouth in the spring of 1913.

Family Chætopteridæ Audouin and Edwards.

Polychæta inhabiting a tube of parchment-like consistency and very closely adapted to their tubicolous life. Body divided into two, or sometimes three, distinct regions. Prostomium small, often bearing eyes; peristomium forming a collar, with two tentacles more or less developed. The first (anterior) region is composed of a small and fairly constant number of segments; of the two divisions of the parapodium the notopodium only is developed. The segments behind this region have biramous parapodia; the variation of the notopodia here affords the chief method of differentiating between the genera of the family. Generally two distinct types are successively met with in the same animal, thus enabling us to distinguish second (median) and third (posterior) regions. Throughout the body the notopodia carry capillary setæ; in the fourth segment one or more are much stronger and thicker than

the rest. Each neuropodium consists of a double ridge, with several rows of uncini. The dorsal surface is greatly flattened in the anterior region, and carries a median ciliated groove, which runs the whole length of the body in some forms, but is interrupted in others.

Table of Genera.

(*a'*) All segments behind anterior region similar.	
(*b'*) Notopodium of posterior segments unilobed	*Ranzania*
(*b''*) Notopodium of posterior segments bilobed	*Telepsavus.*
(*a''*) Median and posterior regions both present.	
(*c'*) Segments in median region with bilobed foliaceous notopodia, each carrying several capillary setæ.	
(*d'*) Number of segments in median region variable ...	*Phyllochætopterus.*
(*d''*) Two segments in median region	*Spiochætopterus.*
(*c''*) Segments in median region typically with unilobed notopodia. Peristomial collar well developed.	
(*e'*) Median segments two or three in number; notopodia all conical in shape; tentacles long	*Mesochætopterus.*
(*e''*) Median segments five in number; first with separate aliform notopodia; others with notopodia fused to form fans or suckers; tentacles short...	*Chætopterus.*

Mesochætopterus, gen. n.

Chætopterids with a well-developed peristomial collar and a pair of long peristomial tentacles. Body divided into three regions. The anterior *contains* 9–13 *setigerous segments; the parapodia are represented by short and conical notopodia with capillary setæ; in the fourth setigerous segment several of the dorsal setæ are enlarged. The* median *region is composed of* 2 *or* 3 *elongated segments, forming dorsally a flat region, with continuous lateral borders, covered with glandular epithelium and ornamented with transverse ridges. Typically the notopodia are rather enlarged, conical, and fleshy, with a groove running down the inner border; the neuropodia are single in the first, double in the succeeding segment or segments, and contain uncini. The* posterior *region contains a large number of segments similar to those in* Chætopterus, *but with much shorter notopodia. A dorsal ciliated groove runs from the mouth along the median line to the posterior end. In one or more of the median segments the lips are enlarged to form a fleshy organ.*

The genus thus agrees with *Chætopterus* in the reduced number and specialised character of the segments of the median region. It resembles *Phyllochætopterus* in the continuous ciliated groove and the long tentacles.

Diagnoses of Species of Mesochætopterus *here described.*

M. taylori, sp. n.—*A long but slender* Mesochætopterus, *living in a long narrow unbranched tube of opaque parchment, embedded for the most part vertically in sand and ending blindly. Prostomium very small, without eyes, entirely surrounded and hidden by the well-developed peristomial collar. The* anterior *region contains* 9 *or*

10 *setigerous segments. The* median *region is composed of* 3 *segments; in all, the notopodia are of the type described in the diagnosis of the genus. The* posterior *region contains a large number* (*about* 60) *of segments; the short notopodia each with several capillary setæ.*

Locality. Pacific coast of North America.

M. minuta, sp. n.—*A very small slender* Mesochætopterus, *living in tubes of a translucent horny material coated with coarse sand. Prostomium large and conical; peristomial collar well developed, but not so complete as in* M. taylori. *Just external to the tentacles is a pair of eyes. The* anterior *region contains* 10–13 *segments. The* median *region is composed of* 2 *segments; the first pair of notopodia are small and clavate, the second pair are of the type described above for the genus. The ciliated groove is expanded into a cup in the middle of the second median segment. The* posterior *region is composed of segments which are double anteriorly, single posteriorly; each notopodium has a single seta.*

Locality. Cape Verde Islands, Atlantic; Torres Straits, Pacific.

Mesochætopterus taylori, sp. n. (Plates I., III., figs. 5, 6, 9; Text-figs. 1–5.)

Occurrence and Habits.—This animal was first found in Departure Bay, near Nanaimo, Vancouver Island, on a wide stretch of sandy beach, which was partly bare and partly covered with beds of *Zostera*. Over the whole area, from the middle of the beach to the lowest tide-mark, there were to be found brown tubes about a quarter of an inch in diameter, lined with a brown parchment-like material, while the outer layer is membranous and coated externally with sand-grains. The tubes, which project very slightly above the surface, are not U-shaped as in *Chætopterus*, but go straight down through the sand generally for about eighteen inches. On reaching the shingle underneath they sometimes turned and ran horizontally. In one case, where especial care was taken to obtain the tube whole and uninjured, it was found to end blindly in a neatly rounded apex. The last part was much thinner, without the parchment lining. The total length of the tube in this case was three feet. It is, as a rule, however, very difficult to obtain the entire tube, owing to the fact that the sand is deeper in most places and the tube runs vertically through its whole extent. But without obtaining the whole tube it is almost impossible to examine entire specimens of its inhabitant, which rapidly retreats to the depths of its dwelling as soon as the spade strikes the sand. Most of the individuals collected consisted only of the first two regions.

Later the animal was dredged in two or three fathoms of water at Nanoose Bay, and also observed on sandy beaches, between tide-marks, at Victoria on the south end of Vancouver Island and Olga in the San Juan Archipelago, just over the

International Boundary. It is thus widely distributed in the neighbourhood of Puget Sound and the Gulf of Georgia.

One whole specimen was obtained with the following dimensions :—

Length 28·5 cm. Width in broadest part 1 cm.
Anterior region with 9 segments 1·8 cm. long.
Median region with 3 segments 4·0 cm.
Posterior region with 68 segments 22·7 cm.

This was probably a small individual, since in others measured the anterior and median regions exceeded the figures given above.

Mesochætopterus is a longer and much more slender worm than *Chætopterus variopedatus*. The delicacy and transparency of the integument, which is so marked a feature of the last-named species, is not characteristic of the new genus. The whole surface is a creamy white or yellow, relieved by dashes of chocolate pigment on the peristomium and tentacles alone. In the posterior region the dark green gut shows through the body-wall. The ventral musculature is, throughout the body, more developed than in *Chætopterus*.

The *prostomium* (Pl. I. fig. 3) is a small rounded prominence with unpigmented skin. It is much more distinct than in *Chætopterus*. There is no trace of eyes. The *peristomium* forms a prominent buccal funnel which entirely surrounds the prostomium. It is, however, shallower, with more gently sloping sides than in *Chætopterus*. As mentioned above, there is here a noticeable development of the chocolate pigment, which does not dissolve in alcohol, and so is retained by the preserved specimens. The peristomial tentacles originate just outside the peristomial collar. They are stout grooved structures (very extensile in the living animal) and measuring, even in their contracted state, 3–4 cm. They contain a pigment similar to that mentioned above. The *mouth* is situated between the prostomium and the ventral lip of the peristomium, and is bordered in some specimens by two rounded lips below.

The *anterior region* is convex on the ventral side, concave on the dorsal. It differs, however, generally from that of *Chætopterus*, firstly in the narrower width and secondly in the shortness of the notopodia. In 21 specimens examined, 10 had 9 segments, an equal number had 10 segments, and a single individual 11. In *Chætopterus variopedatus*, similarly, though 9 is the typical number, Joyeux Laffuie observed individuals with 10, 11, and even, in one case, 12 segments. The parapodia of the anterior region are all similar and represented by the conical notopodia, which increase slightly in size as we pass posteriorly. The dorsal curvature is not so distinct as in *Chætopterus*. The last segment does not bear an appendage representing the neuropodium, such as occurs in *C. variopedatus* (Joyeux Laffuie, **9**, p. 257, pl. xv. fig. 2) and other species.

In the notopodium of *Chætopterus* there are two long straight rows of capillary setæ, embedded for the greater part of their length in the parapodium, but projecting from the surface for short but equal distances. They are all lanceolate in type, but the dorsalmost setæ differ from the rest in being slender and scarcely dilated. This tendency to differential development is greatly exaggerated in the 4th segment. The dorsal setæ preserve their slender lanceolate character, but a number of the ventral setæ become short, strong, truncated at their extremities, and black in colour. Those situated most ventrally present these characters in the highest degree (text-fig. 4 A).

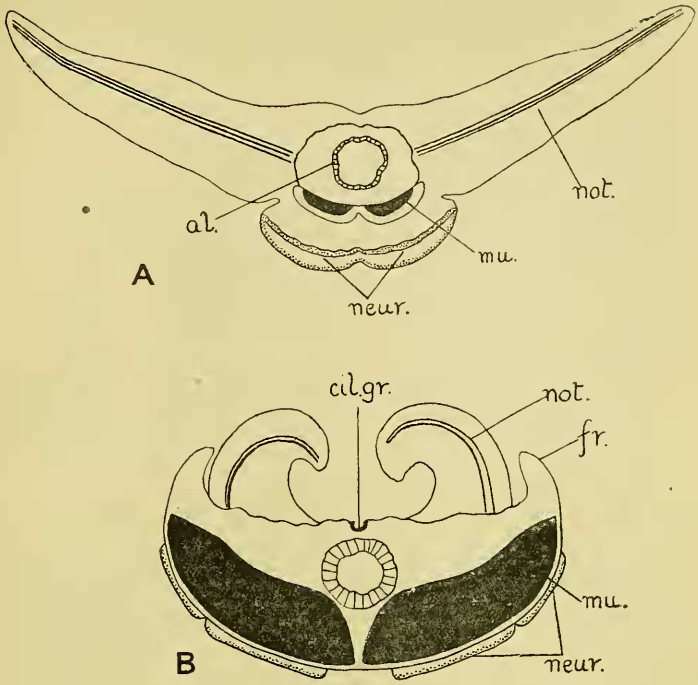
In *Mesochætopterus* the setæ (Pl. III. fig. 9) are more delicate than those of *Chætopterus*, and have a different arrangement, owing to the shortness of the parapodia. They are mostly of a distinct lanceolate type and equal in length, but a few of the dorsalmost are much longer and more slender, projecting in a ragged tuft from the extremity of the neuropodium. They occur in a slightly curved row. In the fourth parapodium there is a single line making a very pronounced curve. Ventrally there are about 12 modified setæ.

Median Region.—Though consisting of three segments only, it is much longer than the anterior region. In *Chætopterus* the median region is characterised by the transparent nature of the body-wall and the reduced width of the segments; here every segment is of a uniform width greater than that of the anterior region, the dorsal surface is flattened and glandular, and enclosed on each side by a continuous border formed by the thin upturned edges of the segments (Pl. I. fig. 2, *fr.*), and the ventral muscles are much larger and stouter than in *Chætopterus*.

When the animal is alive and inside its dwelling the lateral borders are approximated so as to form an imperfect tube dorsally. Their appearance in text-fig. 1 does not do justice to their extent in the living animal.

The parapodia in *Mesochætopterus* have not undergone the great and diverse modification occurring in *Chætopterus* (compare text-fig. 1, A, B). They resemble very closely those of the abdominal region and attain a similar development in all three segments. The notopodia are short and conical, little larger than in the abdomen; they possess an internal skeleton of two or three stout capillary setæ. They are on the distal surface and approximated to the middle line. On the inner surface they possess a ciliated groove which meets the median groove. I think that there is little doubt that they act as accessory organs for the collection of microscopic food, interrupting the dorsal channel, and separating food-particles from the current by the action of the cilia contained in these grooves. The neuropodia are slightly different in the three segments. The ventral surface of the anterior region (Pl. III. fig. 5) is entirely occupied, as in *Chætopterus*, by a "plastron" (*pl.*) with a slightly wrinkled appearance to the naked eye and composed of high epithelial

Text-figure 1.



A. *Chætopterus variopedatus*. B. *Mesochætopterus taylori*.
Anterior view of median segments.

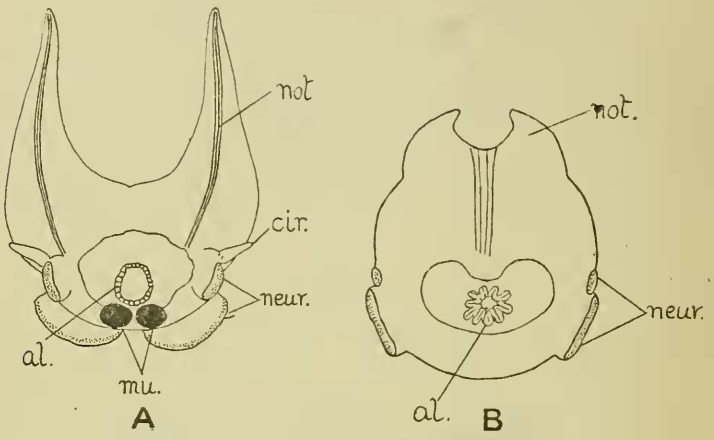
al., alimentary canal; *cil.gr.*, dorsal ciliated groove; *fr.*, lateral borders; *mu.*, ventral longitudinal musculature; *neur.*, neuropodium; *not.*, notopodium with its acicular setæ.

cells. From this, along the median region, there runs a wedge-shaped prolongation (*w.*), which narrows down in the second segment to a median groove. But in the first segment it is broad, and the neuropodia are restricted to two narrow lateral strips of different appearance. Here, then, each neuropodium is a single structure; in the two succeeding segments the neuropodia are much broader, extending almost to the middle line, and are divided into a dorsal and a ventral half, the former being slightly smaller and pushed a little forward. Each contains several rows of uncini. There is no indication whatever of the fusion of the neuropodia to form a sucker-like median structure, which occurs in *Chætopterus*. A typical uncinus of this region is figured in text-figure 3.

The dorsal surface of the median region is covered by glandular epithelium, raised into transverse furrows.

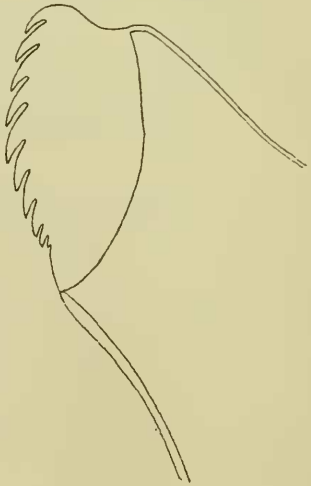
Posterior Region (text-fig. 2).—In the one complete animal which I obtained this contained 64 segments, a much larger number than has ever been observed in *Chætopterus* (Joyeux

Text-figure 2.



A. *Chætopterus variopedatus*. B. *Mesochætopterus taylori*.
To show difference in form of typical segments of the posterior region.
cir., cirrus-like appendage of the neuropodium. Other lettering as in text-fig. 1.

Text-figure 3.



Mesochætopterus taylori. × 325.
Uncinus from first segment of median region.

Laffuie, 9, gives 27–40). The segments differ from those of the median region chiefly in their shorter length. The whole region has the appearance of a string of beads, each segment being rounded and connected with its fellows only by a narrow neck, through which run the intestine and the nerve-cord (Pl. III. fig. 6). The rounded appearance is due to the very much swollen portion of the segment which contains the generative organs. The two notopodia have coalesced for a considerable part of their length, so that the free portions are very short indeed. In them are contained several (about 8) capillary setæ. The neuropodia constitute a continuous narrow ridge half encircling the segment; it bears on each side two uncinigerous tori, which are, however, by no means so well developed and independent as is the case in *Chætopterus*. The dorsal torus is a little smaller and placed rather more anteriorly.

The small cirrus-like appendage (*cir.*) found just outside the dorsal torus in *Chætopterus* is not present in *Mesochætopterus*.

Mesochætopterus minuta, sp. n. (Plates II., III. figs. 7, 8; Text-figs. 4, 5.)

Occurrence.—This species was found twice by Mr. Cyril Crossland during his visit to the Cape Verde Islands in August and September, 1904, once at St. Vincent, and again at Porto Praya. On the first occasion tufts of tubes were collected on the shore (? amongst sand) at low tide, and on the second tubes which contained much larger specimens were found projecting from and embedded in masses of nullipores. They were associated with *Onuphis* and a species of Spionid. In November 1913, I found this species also at Murray Island, Torres Straits, living in sandy tubes between tide-marks. Except for their generally smaller size, these Australian individuals conform with the description which follows in all essential particulars.

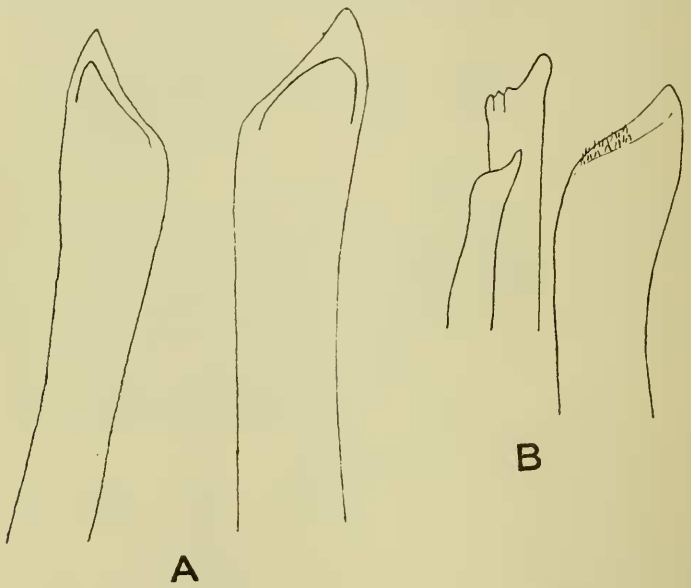
The animal is milk-white in colour, with no pigmentation, except that of the gut shining through posteriorly. None of the individuals which reached me was quite complete, but those from Porto Praya were about 2·5 cm. in length, while those from St. Vincent barely exceeded 1·5 cm. In the largest the maximum breadth was very little more than 1 mm.

The *prostomium* (Pl. II. fig. 4) is a very distinct feature, better developed than in any species of *Phyllochætopterus* which I have been able to examine. It is conical in shape. The *peristomium* forms a deep cup like that in *M. taylori*, but not so complete owing to the size of the prostomium, and without the considerable development of pigment which occurs in the other species. At the base of the prostomium come off the two long peristomial tentacles. The eyes were only seen in the specimens from Porto Praya, in which, however, they were very distinct. They are curiously placed on the peristomium just outside the bases of the tentacles.

In the *anterior region* the number of segments is variable. In

the two larger individuals from Porto Praya there were 13 or 14 respectively; in those from St. Vincent 10 segments in most, 9 in one or two. The notopodia show differences from those in the corresponding region of *M. taylori*, due partly to the great difference in size of the two animals. In the Cape Verde species there is naturally a very much smaller number of setæ in each parapodium (about 20 or 30). The setæ themselves are easily distinguishable from those of *M. taylori* (*cf.* text-fig. 5) by their shorter heads. As in that species so here, dorsally they become longer and more slender, with an almost symmetrical

Text-figure 4.



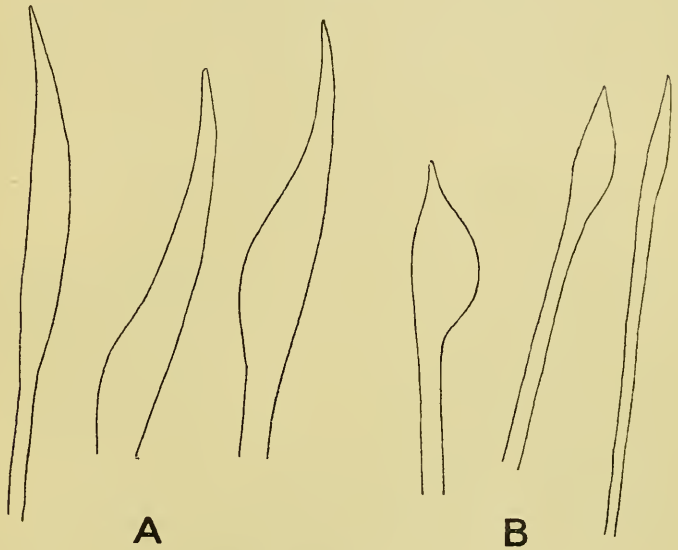
A. *Mesochætopterus taylori*, × 70. B. *Mesochætopterus minuta*, × 325. Enlarged setæ of fourth segment.

lanceolate head. The fourth segment (text-fig. 4 B) carries ventrally a number of dark brown modified setæ varying from 4 to 7. The larger ones have a distinct likeness to those of *M. taylori*, though, of course, they are much smaller. There is a tendency for the oblique edge of the seta to be fimbriated. This is apparently due, not to a natural serration, but to splitting of the fibrous chitin of the seta.

The *median region* consists of only two segments, but it is nearly twice as long as the anterior region. It is the great likeness in the configuration of the median region which shows

quite plainly that these two worms from the Atlantic and the Pacific must be placed in the same genus. In both the segments are broad and flattened, with a glandular dorsal surface raised into transverse ridges and traversed by a continuous ciliated groove. In both, too, the parapodia are similar, and there is an enlargement and incipient modification of the ciliated groove to form a cup-shaped organ. There are, of course, minor differences, namely, in the development of the notopodia of the first segment and in the presence of a rounded lateral border to the region without the thin upturned edges which are characteristic of *M. taylori.*

Text-figure 5.



Typical notopodial setæ of anterior region.

A. *Mesochætopterus taylori.* B. *Mesochætopterus minuta.*

The first segment is much longer. The notopodia are even less developed than in *M. taylori*—in fact, they are merely clavate papillæ like the second pair of peristomial appendages in *Phyllochætopterus.* In the individuals I examined there were two or three slender setæ embedded almost entirely in the notopodium, but projecting very slightly from the surface and ending in a slight lanceolate head.

The neuropodium is a single structure, separated from its fellow on the other side by a wedge-shaped prolongation of glandular tissue exactly like that described above for *M. taylori.* The uncini contained in the neuropodium are very similar to

those of the other species, though much smaller. But they have six or seven teeth, or very nearly the number which is found in *M. taylori*.

The second segment is about two-thirds the length of the first. The notopodia of this segment are exactly like those described as typical for the genus—conical and enlarged, with a groove running down the internal border towards the median groove. It contains a couple of slender acicular setæ, which do not project terminally from the parapodium as in the first segment and have no distinguishable head. The neuropodia are double structures and call for no remark.

About the middle of this segment there is an enlargement of the lips of the ciliated groove rather like those occurring in the second and third median segments of *M. taylori*. It is exceedingly interesting to notice, however, that in some individuals the lips approximate posteriorly, and an almost complete circular cup is formed like that in the 13th segment of *Chætopterus*. This is a variable character in the species, however—in the individual figured here there is no posterior fusion of the lips. But from the variations which occur in the genus *Mesochætopterus* we can undoubtedly see how the accessory feeding-organ in *Chætopterus* has arisen from the ciliated groove.

The *posterior region* (Pl. III. figs. 7, 8) is composed of short rounded segments. As none of the specimens is complete, I am unable to say how many are found. Anteriorly each segment is divided into two by a slight constriction. The proximal half bears the parapodium. As in *M. taylori*, the free part of the notopodia projects very slightly from the surface. As a rule, they contain a couple of thin acicular setæ, sometimes only a single one. The neuropodia have the usual double uncinigerous torus, the dorsal part being very small.

The distal half of the segment is the part which in *M. taylori* is diminished to form the neck between successive segments.

The two species here described differ extraordinarily in size, for while *M. taylori* is the largest Chætopterid known, *M. minuta* is probably the smallest. I shall have occasion to remark upon the great variation which occurs in the development of the prostomium in the genus *Phyllochætopterus*, but in this respect these two species differ still more widely. But while *M. minuta* resembles many species of *Phyllochætopterus* in the character of the prostomium, the peristomial collar is deeper and better developed than is ever the case in the latter genus, and the second pair of peristomial appendages—which are so characteristic of *Phyllochætopterus*—are, I think, absent here. These two circumstances are, I believe, connected. Then, again, the number of segments comprised in the median region is quite constant, but different in the two species—two in *M. minuta*, three in *M. taylori*,—and this draws another very definite distinction. There are other differences, which I have mentioned above. Some of these, *e. g.* number and shape of setæ, are partly dependent

upon the differences in size of the animals. Speaking generally, however, these two species are far more definitely distinguishable than any pair of species in *Phyllochætopterus* or in *Chætopterus*.

No less interesting than the diversity in form of the two species is their curious distribution. While *M. taylori* is so far only known to occur in the coastal waters of the N.E. Pacific, *M. minuta* has already proved to have a much more extended range. The type-specimens come from the subtropical regions of the North Atlantic, but I was surprised to find a *Mesochætopterus* of common occurrence in Torres Straits, which is, without doubt, identical with *M. minuta*. It will prove, I venture to predict, a widely spread Indo-Pacific form, and its absence from previous descriptions only illustrates the difficulty of obtaining a representative idea of a Polychæt fauna from general collections. Though *M. minuta* may be found in the Indian Ocean, it is less likely to turn up in the Red Sea and the Mediterranean, where so much attention has been given to the obscurer forms of Polychæt worms, and the distribution will probably remain discontinuous in type.

The Position of Mesochætopterus *in the Family.*

It can hardly be doubted that a close relationship exists between *Chætopterus* and *Mesochætopterus*. The structural differences between them correspond closely with the different kinds of tubes which they occupy. *Chætopterus* possesses a much wider tube, in which it fits very loosely, and it is for this reason that the excessive and bizarre modifications of the median region have been produced. Adhesive organs are needed to maintain the position of the worm in the tube, and these are formed by the fusion of the notopodia giving a cup-shaped sucker. Ciliary action alone would be too feeble to produce an efficient circulatory current in so wide a space, and hence the fans of the 14th–16th segments exist. The notopodia of the anterior and posterior regions are concerned in the movement of the animal up and down in its tube. They must be long enough to touch the walls and so attain to much greater dimensions than in *Mesochætopterus*. The greater or lesser length of the parapodia causes, as we have seen above, some difference in the arrangement of the setæ.

Chætopterus possesses, too, a complicated method of feeding, which is responsible for further differentiation in its external structure. This method has been lately described by Enders in detail (4). The long aliform notopodia of the 12th segment and the dorsal cup of the 13th segment alike aid in separating food from the respiratory current, and compacting it into masses which are swept forward in the ciliary groove to the mouth. The middle region, then, fulfils a double function in promoting the circulation of water in the tube and collecting food, different segments being specialised for each task. In consequence of this

division of labour, a number of segments is included in the region, larger than in *Mesochætopterus*.

I have not found it possible, in the absence of experimental observations, to reach any such clear conclusions as to the functions of the different organs of *Mesochætopterus*. Food is partly collected by two long grooved tentacles, which are constantly projecting from the mouth of the tube and sweeping over the surface of the sand in search of small fry. Enders makes a similar observation on another Chætopterid with long tentacles, to which he applies the name *Spiochætopterus oculatus*? He describes it as scraping with its tentacles the sides of the aquarium in which it was kept; the diatoms thus dislodged were swept up the ciliary grooves of the tentacles into the mouth. Nutritive particles are, no doubt, also collected by the action of the cilia of the buccal funnel as in *Chætopterus*, and, lastly, I think, the notopodia of the median region have a similar function to those of the 12th segment in the above-mentioned worm. A branch of the median ciliated groove runs along the inner surface of each of them, and in my view such minute organisms as are not strained from the circulating sea-water anteriorly are here arrested by the parapodia, mixed with mucus secreted by the glandular epithelium of the surface and swept into the median groove and along to the mouth.

The ciliated groove in *Mesochætopterus*, as in *Phyllochætopterus*, is quite continuous in its course from the head to the tail. The primary function of such a groove is to maintain a respiratory current through the tube, as is well seen in forms with a transparent dwelling like *Phyllochætopterus prolifica*.

In *Chætopterus*, owing to the development of the respiratory fans, the ciliated groove does not extend farther back than the 13th segment and has changed its function, being now employed in the collection of food. We may well suppose that in *Mesochætopterus* the action of the cilia causing a flow of water from head to tail is not continuous, but is reversed on occasion to carry food back to the mouth.

Chætopterus is without doubt the form most specialised in structure in the family, and this is shown not only by the modifications of the median region but also in the discontinuous ciliated groove and the shortness of the tentacles. It is impossible to agree with Enders, who supposes that the long tentacles of *Spiochætopterus* "have undergone a considerable specialisation" and speaks of the shorter tentacles of *Chætopterus* as more primitive than those of *Spiochætopterus*.

The group of Chætopterids, which includes *Ranzania*, *Phyllochætopterus*, *Telepsavus*, and *Spiochætopterus*, are distinguished by possessing long tentacles (the most important organs in procuring food) and a complete ciliated groove. A differentiation of the median from the posterior region is sometimes not found at all (*Telepsavus*, *Ranzania*). If it occurs, the number of segments in the median region is very variable (in species and even in

individuals), and they differ very little from the abdominal segments. But the other two points are, without doubt, primitive characters, and the long tentacles (but not the ciliated groove) are shared with the Spionids.

Mesochætopterus forms the connecting-link between these primitive forms and the specialised *Chætopterus*.

In the possession of long tentacles and a continuous ciliated groove it resembles *Phyllochætopterus*. In the development of a very distinct median region composed of a small number of segments with grooved notopodia, which possibly assist in the collection of food, it comes near to *Chætopterus*.

Telepsavus Gabr. Costa.

Only two species of this genus have been described hitherto: these are *T. costarum* Claparède, from Naples (**1**), and *T. bonhourei* Gravier, from Djibouti in the Red Sea (**5**).

Telepsavus sp. (Text-figs. 6–8.)

Though this Polychæt is a very common and widely distributed member of the beach fauna of British Columbia, my collection contains only one specimen which is at all well preserved, and in this the head is incomplete. Such individuals as were preserved in their tubes were quite worthless, owing to the impermeability of the material, which thus differs from that formed by *Phyllochætopterus* considerably more than their appearance seems to show. The following account of the species is thus very incomplete, and I refrain from giving a name until the species can be better defined. I should also like to state my opinion that the validity of Gravier's species is questionable until an actual comparison of the Mediterranean and Red Sea forms is made.

Occurrence.—On the same sandy beach at Departure Bay, which I have described in my account of *Mesochætopterus*, the tubes of a second smaller Chætopterid were discovered. They are composed of a translucent horny material and are annulated, the joints occurring at short intervals. In length they sometimes exceed a foot and a half, running vertically down through the sand and ending in a neatly rounded apex. In diameter the tube is less than 2 millimetres, the worm fitting fairly tightly within its habitation. A single individual occurs in each tube, with its long peristomial tentacles often projecting from the aperture.

The distribution of *Telepsavus* has been found to be a wide one. Generally it may be said to occur wherever *Mesochætopterus* exists. I have collected both together in Departure Bay, at Olga in the San Juan Archipelago, on Ballard Beach, Seattle, U.S.A., and by dredging in two or three fathoms of water at Nanoose Bay, Vancouver Island.

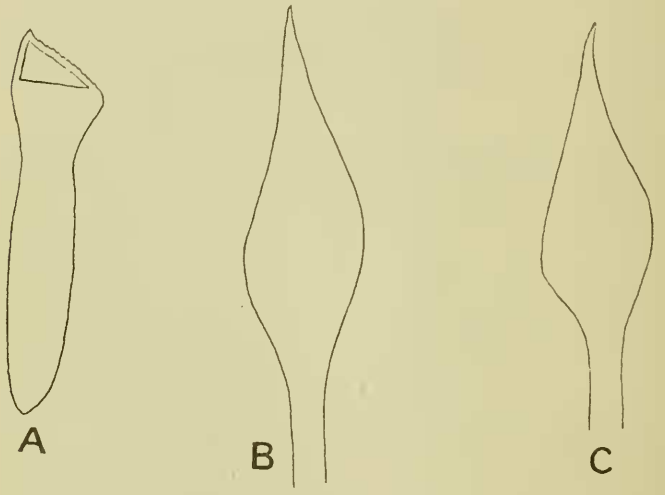
At the end of August 1911, too, I found *Telepsavus* at Skidegate in the Queen Charlotte Islands, 500 miles to the north, living in muddy gravel. Here and at Departure Bay at the

beginning of the month the female worms had well-developed orange gonads.

Size.—The almost complete individual measured was about 5 cm. long and nearly 2 mm. broad (*i. e.* about the same length as and rather broader than the two species hitherto described).

I cannot, unfortunately, say anything about the structure of the *head*. The *anterior region* consists of 9 segments. In my specimen the 7th, 8th, and 9th segments, but particularly the two latter, are much longer than the others. In this particular the Canadian form agrees with the description of *T. bonhourei*,

Text-figure 6.



Telepsavus sp.

A. Enlarged seta from 4th segment. × 70.

B, C Notopodial setæ from 5th segment. A lanceolate type occurring in a dorsal position. × 325.

while the figure of *T. costarum* shows little of such a differentiation. I should like, however, to assure myself of the importance of this point (which is strongly emphasised by Gravier) on more and better material and by a comparison with specimens from Naples.

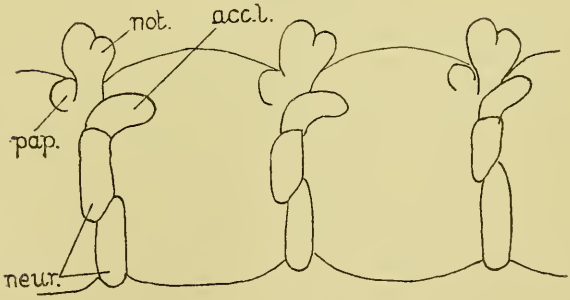
In the 4th segment there is a single greatly enlarged seta (text-fig. 6 A). The point of this is an irregular triangle. The base is slightly curved and quite entire (in *T. bonhourei* it is furnished with a fringe of projecting points). The longer of the outer sides is furnished with very unequal serrations. There is also an auxiliary bundle consisting of a few fine setæ, such as is figured for *T. costarum*, while it is expressly stated that it does not exist in *T. bonhourei*. A series of types of notopodial setæ is shown in text-fig. 7.

Text-figure 7.

Telepsavus sp.

Other types of notopodial setæ from anterior region. × 325.

Text-figure 8.



Telepsavus sp.

Lateral view of posterior region.

not., notopodium ; *acc.l.*, accessory lobe of this : *pap.*, papilla of unknown nature; *neur.*, neuropodium.

Behind the anterior region there are between 30 and 40 segments. all of the same type with a bifid notopodium (text-fig. 8). The first three segments are distinctly longer than the rest, and

there is no such development of glandular papillæ on their dorsal surface as is figured in the Neapolitan species (but absent in *T. bonhourei*). The parapodia throughout consist, as is usual, of a bifid notopodium with capillary setæ, a lateral accessory lobe such as occurs in *Phyllochætopterus*, and a double neuropodium consisting of two adjacent uncinigerous ridges. There is, moreover, in all the segments a very distinct, occasionally double, papilla just anterior to the notopodium. This may be the nephridial papilla, but, if so, its position is more dorsal than usual.

The ventral surface of the anterior region is deeply tinged with a brown to purple pigment. In this it apparently resembles *T. costarum*, while in *T. bonhourei* the 7th segment alone is markedly pigmented.

From the points which have been stated here it will be seen that the form certainly differs specifically from *T. bonhourei* and probably also from *T. costarum*.

Phyllochætopterus Grube.

Phyllochætopterus prolifica, sp. n. (Plates IV., V.; Text-fig. 11.)

Phyllochætopterus *of small size (1–3 cm. in length), with eye-spots. Anterior region usually with 12 setigerous segments; a single enlarged seta in each parapodium of the 4th segment. Median region with a very variable number of segments. In segments of posterior region each notopodium contains a single seta. Tubes creeping, usually containing several individuals and possessing several short branches opening to the exterior.*

This species of *Phyllochætopterus* was first collected outside the harbour of Nanaimo. Here, as was proved by frequent dredgings between the Five Finger Rocks on the north and the island of Gabriola to the south, the muddy bottom is covered with a thick growth of hexactinellid sponges (*Bathydorus dawsoni*, *Aphrocallistes whiteavesii*), and associated with these are the thin and delicate tubes which prove to contain *Phyllochætopterus*, sometimes sparsely scattered, sometimes in such thick and tangled masses that the dredge contained little else. Later in the year, a visit to the Marine Biological Station of the University of Washington at Friday Harbour showed that this annelid occurs abundantly in various localities in Puget Sound. It was dredged at many points in the San Juan Archipelago and found associated with very different companions. In the dredgings from deeper water (down to 60 fathoms) masses of large barnacles (*Balanus aquila*) and the tubes of the Polychæt *Sabellaria* also occurred; in shallower waters (up to 5 fathoms) the *Phyllochætopterus* tubes were entwined with red seaweeds. But though the vertical range as seen above is fairly notable, it never occurs above low-tide mark, where it is succeeded by the other members of the family, *Mesochætopterus* and *Telepsavus*.

The fact that though so abundant this Phyllochætopterid has remained up to the present undescribed is due to the slender nature of the tubes, which easily escape identification as the habitation of an annelid, and to the difficulty of preservation.

In its wide distribution and its habit of forming intertwined masses of tubes, *P. prolifica* resembles *P. socialis* of the Mediterranean, of which Claparède wrote in 1866 : "Cette annélide est probablement l'espèce la plus abondante dans le golfe de Naples*, où ses tubes juxtaposés, grisâtres, papyracés et enchevêtrés les uns dans les autres par leur extrémité postérieure, paraissent former d'immenses prairies. Du moins les pêcheurs apportent-ils à première requisition, sous la nom de *ceppa grande*, des piéces qu'on prendrait pour de grands quartiers de gazon, et qui sont formées presque exclusivement par les tubes de ce Phyllochétoptère." In *P. pictus*, too, described by Cyril Crossland (2) from Zanzibar in 1903, a similar habit was observed. On the occasion of its discovery the tubes "were found clustered together in considerable numbers on the underside of a large stone at low-water level." But in the remaining species of the genus hitherto described the worms inhabit straight solitary tubes.

As will be seen later, examination of the individuals of *P. prolifica* shows that the size and external characteristics of the species tally fairly well with the description of *P. socialis*. But that there is a deeper physiological connection is indicated by the occurrence in both species of more than one individual in a single tube. The phenomenon of asexual reproduction, which Claparède suggested as the cause of the colonial habit in *P. socialis*, I wish to record here as the outstanding feature of *P. prolifica*.

I will first give Claparède's statement on this point which follows immediately after the passage quoted above :—" L'étude de cette annélide a fait surgir quelques curieux problèmes physiologiques. Les *ceppe grandi* qu'apportent les pêcheurs sont formées exclusivement par des individus d'un même sexe, généralement des mâles, les femelles étant à ce qu'il semble beaucoup plus rares que les mâles. En outre, chaque tube est régulièrement habité par deux ou trois individus, tous adultes et mûrs. Le tube est cependant si étroit que seul l'individu antérieur peut fait sortir ses tentacules par l'ouverture, tandis que les suivants sont emprisonnés derrière lui. Dans de pareilles conditions, on doit supposer tout naturellement que ces derniers ont été engendrés par bourgeonnement postérieur à l'extrémité du premier, et que peut-être même tous les individus d'une même *ceppa* sont nés par gemmation. Toute-fois je n'ai pas réussi à vérifier l'exactitude de cette hypothèse. Je ne suis pas même très-certain des rapports des tubes entre eux. Ces petites habitations cylindriques larges à peine d'un millimètre et longues parfois de 8 à 10 centimètres, sont irrégulièrement contournées dans leur partie postérieure, sondées les unes aux autres, et ne peuvent se séparer sans

* I understand that *P. socialis* is now considered something of a rarity at Naples.

déchirures. Il m'a semblé quelles s'anastomosaient parfois, cependant j'éprouve quelque hésitation à affirmer ce point. Il y a donc, on le voit, encore bien des questions à vider au sujet de ces vers."

The incompleteness of Claparède's observations leaves us in some uncertainty with regard to *P. socialis*. As I understand the foregoing passage, he was unable to assure himself as to which of the following alternatives was correct. Either;

(1) There are a number of unbranched tubes packed close together, but without connection, each tube containing two or three individuals, but having only a single opening;

Or else (2) these adjacent tubes are in reality connected with one another, and the whole bundle of tubes (*ceppa*) is a single colony, all the worms contained in which have probably been budded off from a single original individual. This is supported by the fact that the worms in a bundle are all of the same sex.

In *P. prolifica*, on the other hand, the relations of the tubes are perfectly clear. Where they come into contact they do not adhere in the complex manner described by Claparède. In the following paragraph I state shortly the conditions which are found in the colonies.

The tubes are comparatively long and sometimes divide into two or more branches of approximately equal length. Most contain more than one worm and some as many as six. The main tube is provided with several short branches which open to the exterior, but the number of openings does not correspond to the number of worms in the tube. The worms can change their position in the tube fairly rapidly and can turn round and pass each other. Those individuals which occupy a favourable position protrude their long tentacles from one of the openings to assist in the collection of food.

It occurred to me on first observing the above facts, while I was still unaware of Claparède's observations on *P. socialis*, that an explanation was probably to be found by supposing some sort of asexual reproduction to occur in the species. The nature of this reproduction was indicated by a discovery made during an early examination of the living material at Departure Bay. I was surprised to find emerging from freshly dredged tubes very short individuals which differed considerably from the normal forms in the constitution of their bodies. One of these only measured 6 mm., which is $\frac{1}{3}$–$\frac{1}{4}$ of the normal length. The segments of which it was composed were arranged as follows:—

Anterior region	.....	8 segments.
Median ,,	.....	2 ,,
Posterior ,,	.....	20–30 ,,

Not only did the anterior region consist of less than the normal number of segments (12), but also there was no segment with a modified seta such as occurs in all adults of the species, and the peristomial tentacles were represented by minute stumps. The number of segments in the median region was exceedingly

small, but the segments themselves both here and in the posterior region were normally developed, while there could not be the slightest doubt but that the anterior region was in process of regeneration.

A second individual found at the same time gave another stage in the phenomenon. It was more nearly the normal size. The regions contained the following numbers of segments:—

Anterior region.....	11	segments.
Median ,, ...	5	,,
Posterior ,, ...	20–30	,,

The anterior region thus contained nearly the normal number of segments, but it was shorter than usual and the peristomial tentacles were less than half the usual length. This seemed a second case in which the anterior region was regenerating.

On returning to Cambridge, a detailed examination of a large amount of material preserved in formalin was made. Tube by tube was taken and slit up, and the length and constitution of the three regions noted in all the individuals contained therein. It was quite clearly shown that living constantly though the animals do within the shelter of a tube, regenerating specimens are frequently found. From an examination of these it seems certain that a fragment of *Phyllochætopterus* containing only segments of the median and posterior regions easily regenerates an entire anterior region. The number of cases in which this phenomenon has apparently occurred, and the fact that in their protected situation regeneration after external injury is an unlikely event, leads me to suppose that these animals have the power of autotomy and that it is exercised for the distinct purpose of reproduction.

The tables which follow present the results of the detailed examination of several tubes, each represented by a separate

TABLE I.

	Constitution of the three body regions.			
	A. Anterior.	B. Median.	C. Posterior.	Total length of worm.
No. 1.....	12	6	5	1·3 mm.
No. 2.....	12	7	none	1·8 mm.
No. 3 ..	Small regenerating stump 1 mm. long; segments not sufficiently differentiated to count.	5	32	...

table. The figures in the columns A. B, and C indicate throughout the numbers of segments in the regions referred to.

In this tube (Table I.) from Departure Bay Nos. 2 and 3 appear to be complementary, and represent an individual broken in two in the median region. While, however, the median segments of No. 3 have already regenerated a short and undifferentiated region, those of No. 2 have not yet attempted to form a posterior region. The regenerating end of No. 3 is figured in Pl. V. fig. 12, and it will be seen that a number of segments have been marked off by furrows, but that parapodia and setæ have not yet developed. The peristomium is indicated by the rudimentary tentacles. It will be noticed that almost the full number of segments is established at once, and apparently development proceeds simultaneously in each of them.

Table II.

	A.	Length of A*.	B.	C.	Total length.
No. 1 ...	11	5·5 mm. ($\frac{1}{4}$)	10	12	20 mm.
No. 2 ...	9	4 mm. ($\frac{1}{4}$)	8	22	15 mm.
No. 3 ...	12	2 mm. ($\frac{1}{9}$)	8	40	17·5 mm.
No. 4 ...	12	4 mm. ($\frac{1}{5}$)	4	28 (+ number of very small segments)	19 mm.
No. 5 ...	12	6·5 mm. ($\frac{1}{3}$)	14	20	21 mm.
No. 6 ...	12	...	3	20	16 mm.

Another tube from Friday Harbour (Table II.) contained six individuals, all of which with one exception were well-developed and complete specimens. It will be seen that while the number of segments is more constant in the anterior region than in the other two, its length varies very considerably and bears no definite relation to the total length of the body. In No. 3 (Plate V. fig. 13) it is extremely short, although it possesses the usual number of segments, which are of normal width and have the full development of setæ. There is, however, no strengthened seta in the fourth segment, and the peristomial tentacles are about half-grown.

In the other individuals the length of this region varies from 4–6·5 mm.

* The fraction in this column represents the proportion borne by the length of A to the total length.

TABLE III.

	A.	Length of A.	B.	C.	Total length.
No. 1 ...	12	6 mm. ($\frac{1}{5}$)	8	26	30 mm.
No. 2 ...	...	...	...	13	6 mm.
No. 3 ...	...	a very small regenerating stump.		22	12 mm.
No. 4 ...	12	5·5 mm. ($\frac{1}{4}$)	10	10	24 mm.
No. 5 ...	12	6 mm. ($\frac{2}{9}$)	7	22 + 15 very small segments.	27 mm.

In this colony (also from Friday Harbour) there are three worms complete anteriorly and two fragments, one of which is commencing regeneration. Of the first-mentioned, however, No. 4 has probably lately suffered the loss of posterior segments, as shown by the small number of those remaining and the moderate total length. No. 5 is interesting from the possession of a tail of very small posterior segments following others of normal size, and these must represent regeneration after autotomy.

From the comparative rarity of regenerated tails in autotomised worms, it is evident that the anterior region is re-formed much more quickly than the posterior. With regard to the median region, there are two facts which seem to show that regeneration of new segments of this type takes place but rarely. These are :

(1) the great variation in the number of segments (from 4 to 14), even in individuals with well-developed anterior and posterior regions, and

(2) the absence of segments of two different sizes in the region. I have, however, examined one animal alive in its tube in which the normal segments of the median region were preceded by a single newly formed segment of similar type, but only about half the size of the others. I cannot say whether the anterior region was fully formed or not. Cases of regeneration of median segments then do exist, if but rarely.

The facts incline me to suggest that asexual generation only occurs successfully when fragmentation takes place in the median region, that regeneration proceeds both on the anterior and posterior surfaces of the plane of rupture, however small a number of segments are left on one side, but that these median segments usually regenerate anterior or posterior segments, and

only segments like themselves when the other two regions have been completed.

Fragments consisting of segments of the posterior region alone are, however, occasionally met with, and in one case (Table III. No. 3) a minute regenerating stump was found. At the same time there is no evidence that complete regeneration occurs from abdominal segments alone.

Another case may be mentioned in which autotomy had occurred in the middle of the anterior region and a number of segments of smaller size were superimposed on the older segments.

Plate V. illustrates two well-marked regeneration stages of the anterior region from individuals mentioned above, and they should be compared with the individual of normal development shown on the same plate (fig. 14).

Regeneration in *Chætopterus*.

Since the above was written, I have read the observations of Gravier on autotomy and regeneration in *Chætopterus variopedatus*. When an individual is seized by the anterior part of the body, or when it is strongly irritated, rupture takes place between the first and second segments of the median region—this being the place of least resistance. The anterior fragment can reproduce all the rest: the posterior has not always been regarded as capable of regeneration. But Gravier (6) describes and figures a posterior fragment, collected at Saint Vaast-la-Hogue, which carries a regenerated anterior region fully differentiated but quite minute. Gravier's drawing (*l. c.* fig. 2, p. 147) resembles almost exactly those I have given for *P. prolifica*. The whole anterior region hardly equals in length a single original segment, but it possesses a buccal funnel and peristomial tentacles, and the lateral border is marked out into segments, 12 conical seta-bearing notopodia being present on each side. Only in the 4th segment the special setæ are not indicated, and the peristomial tentacles are unequally developed. There are some irregularities, also, in the notopodia, but, generally speaking, they are of nearly equal development. Only the last segment is markedly smaller than the rest, which thus appear to be marked off nearly simultaneously. The total number of segments is 12, while the normal number is only 9. Individuals with 12 segments are very exceptional, and it is curious to find that in regeneration the maximum number of segments should be formed.

The first segment of the median region is present, but in a very rudimentary condition. Noto- and neuropodia are visible, but it has obviously been formed after the segments of the anterior region.

If we summarise the phenomenon so far as it is known in *Chætopterus*, it may be said (1) that autotomy occurs sometimes

as the result of an unexpected stimulus*; (2) that, following autotomy, regeneration will take place from the posterior fragment, the median region thus giving rise to the whole of the anterior region, and after that replacing the missing median segment.

There is thus a clear resemblance to the manner of regeneration in *Phyllochætopterus* and also a clear minor distinction, the presence of a definite breaking-point in *Chætopterus* and its absence in *Phyllochætopterus*. Autotomy and a complete type of regeneration are thus to some extent characteristic of the family Chætopteridæ. In *Phyllochætopterus prolifica*, however, the occasions on which autotomy takes place are so frequent and regular as to subserve a definite method of asexual reproduction. But the nature of the stimuli which cause autotomy, and the question whether the phenomenon is in any sense under the control of the animal itself, can hardly be approached as yet.

Some advantage may, I think, be gained by comparing the cases of regeneration studied in other Polychæta with a differentiation of regions. Ivanow (8) and other authors have made a very thorough examination of these phenomena in the case of the Sabellid *Spirographis spallanzanii*. Here there are three regions: the *anterior thoracic* with the prostomium, bearing the enormously developed tentacles, and the first three setigerous segments; the *posterior thoracic*, consisting of eight or nine following segments; and the *abdominal*, with an indefinite number of segments. Only such fragments regenerate as consist of abdominal segments or of abdominal and thoracic segments. Those containing thoracic segments only always disintegrate. In regenerating fragments, the hinder end always produces abdominal segments, and the anterior end regenerates the prostomium and the three anterior thoracic segments. The posterior thorax develops later by the metamorphosis of the most anterior abdominal segments, a striking change taking place in the characters of the parapodia. The dorsal uncini are replaced by capillary setæ, while in the neuropodium the capillary setæ are replaced by uncini.

A similar phenomenon has been described by Watson (12) in *Potamilla reniformis*, another Sabellid. Here, in the regeneration of the anterior region from abdominal fragments, the prostomium and *one* new setigerous thoracic segment only are formed as a new growth: all the rest of the thoracic segments are formed from abdominal segments in which a modification of the parapodia like that described above occurs. It is curious that two regions, differing from each other so little in morphological characters as do the anterior and posterior thoracic regions of *Spirographis*, should have such a dissimilar method of re-formation.

Though my observations on regeneration in *Phyllochætopterus*

* In 1913, at Plymouth, I noticed that of a tubful of *Chætopterus* which had been brought in, after being kept on board a trawler for 20 hours or so, nearly all had autotomised, as a result of the unhealthy conditions, rupture taking place between the first and second segments of the median region.

are incomplete, it seems probable that the phenomenon here runs a very different course. The three regions of the Chætopterid have no probable connection with those of the Sabellid, nor is there any reason that they should behave in a physiologically similar manner. In *Phyllochætopterus* it seems fairly certain, as I have pointed out above, that regeneration takes place most often from fragments containing median as well as posterior (abdominal) segments, and in all cases the full number of segments in the anterior region is budded off. But, while in both Chætopterids and Sabellids the anterior region is restored by regeneration, in the former family the median region is not completely re-formed as is the case in the latter. The number of segments in the median region is so variable in number that for this and other reasons I am inclined to suppose that regeneration does not take place here, or only very slowly. There is certainly not the slightest evidence, in any regenerating individuals which I have examined, of a transformation of the posterior (abdominal) segments into median segments, such as characterises the Sabellids.

The Possibility of Asexual Generation in *P. pictus*.

The case of *Phyllochætopterus pictus* described by Crossland has already been mentioned. It will be interesting here to quote some figures which Crossland gives to show the variability in the numbers of segments in the anterior (A) and median (B) regions. Eight individuals were examined. They are indicated by the Roman numerals running across the page :—

	I.	II.	III.	IV.	V.	VI.	VII.	VIII.
A ...	15	16	..	13	15	12	15	13
B ...	7	9	5	7	5	3	8	...

Here, too, it will be seen that the median region is much more variable than the anterior, the numbers ranging from 3–9 for a very small sample of individuals. In view of this and the fact that the annelid inhabits clusters of tubes, the relations of which are difficult to make out, I think it is possible that asexual generation occurs here too.

Miscellaneous Observations on the Habits of *Phyllochætopterus prolifica*.

Owing to the transparency of the tube, in the younger colonies at least, it is possible to see something of the movements of the worm within. It shifts its position in the tube by the alternate relaxation and contraction of the body; when contraction occurs, the setæ of that part of the body affected are braced against the sides of the tube. The setæ of the abdomen can be definitely

used as organs of progression, pushing the animal along. The worms can thus move with some rapidity, and they can also turn within the tube and even pass each other. When at rest they generally lie with the long tentacles projecting from an aperture evidently questing for food. All the inhabitants of the tube may not be able to obtain such advantageous situations, but from their activity within the tube it is evident that a frequent interchange of position does take place. The worms do not all lie the same way, so it is difficult to see how a constant and sufficient circulation of water can be maintained through the whole tube. Probably at times the animal is entirely quiescent and the respiratory current interrupted. In all the animals I observed, the action of the cilia in the dorsal groove and of the notopodia of the median region is responsible for a current running posteriorly, which supplies not only oxygen but also food, as in the other Chætopterids. This action is sometimes vigorously supplemented by the undulatory movements of the abdomen. This energetic action—a phenomenon often observed, too, in *Chætopterus*—is possibly necessary for removing objectionable particles from the neighbourhood of the body. In *P. anglica* and to a less degree in *P. prolifica*, it may be seen, however, that the circulation of water is not always thorough, for large sections of the tube behind worms are blocked by fæcal masses, and this may eventually necessitate the abandonment of the old parts and extension of the colony.

I have not observed any individuals bearing genital products, but this is probably due to insufficient examination, and I should not like to suggest that asexual generation has supplanted the sexual method. Isolated individuals (like those of *Chætopterus*) are not able to manufacture fresh tubes in spite of copious secretion of mucus, and new colonies must be formed in the first place by a single individual developed from a fertilised egg, though this, by fragmentation, gives rise to all the inhabitants of the colony. Claparède made the interesting observation that, in *P. socialis*, all the worms in a bundle of tubes developed genital products of the same sex, indicating that they were all derived from a single sexually produced embryo.

Some Points in the Morphology of the Chætopteridæ.

Variation in Form of the Notopodia.— Behind the anterior region of the body both notopodium and neuropodium are present in the parapodium. In nearly all cases the neuropodium is stable and retains its character as a double uncinigerous ridge. In *Mesochætopterus*, where the first neuropodium of the median region is single, there is a slight modification, and in *Chætopterus* the neuropodia of opposite sides in the median region are fused to form a sucker.

The notopodium, on the other hand, is very variable, and it

may be of some service to arrange the different types in a tabular form :—

- A single lobe without setæ ..... — *Ranzania*, 16th and all succeeding segments.
- A single conical lobe with setæ.
  - A single seta ..... — Most species of *Phyllochætopterus* in the posterior region.
  - Several setæ ..... — *Chætopterus* and *Phyllochætopterus aciculigerus, claparedei* in the posterior region. *Ranzania*, 13th and 14th segments.
- A bilobed foliaceous structure with several capillary setæ.
  - *Phyllochætopterus*, in the median region. — A conical or aliform grooved structure (with several capillary setæ).
  - *Telepsavus*, all segments behind the anterior region.
    - *Chætopterus*, 1st segment of median region.
    - *Mesochætopterus*, median region. The two notopodia of the segment fused to form a fan-like structure.
    - *Chætopterus*, segments 3–5 of median region.

The structural types can thus be arranged in a neat series, and there is some evidence to show the direction in which evolution has taken place. Both the conical and the foliaceous types are adapted, the one for progression in the tube, the other for the respiratory function. But since the median region has been clearly developed from the posterior, and the conical type of posterior notopodium is far more widespread than the foliaceous type (*Telepsarus* alone), it seems reasonable to regard the conical notopodium as the more primitive. In this case, *Telepsarus* is a specialised form, in which all the posterior segments have developed foliaceous notopodia and the original type has been lost. But *Ranzania*, though the parapodia are unilobed throughout the body, is not to be regarded as the primitive form from which the Chætopterids diverged. The absence of setæ from most of the posterior notopodia and of long tentacles may surely be regarded as secondary. The 13th and 14th segments are so distinct from the rest as to almost merit inclusion in a separate median region.

The Head in the Chætopteridæ.

In the structure of the head there is also a certain amount of variation in the family. The *prostomium* is in most cases provided with eyes, but it is small in all forms and almost surrounded by the *peristomium*, which forms a collar. In *Chætopterus* and *Mesochætopterus* this collar is so complete as almost to hide the prostomium, while in *Phyllochætopterus* it is incomplete dorsally and shallow, allowing the prostomium to be seen easily. The peristomium gives rise to a pair of tentacles which vary greatly in length, and in *Phyllochætopterus* there is also a second pair of

structures which are generally stated to be tentacles. They are very small flat organs, lying on each side of the prostomium, and generally covering the eyes. Claparède showed, in the case of *P. socialis*, that they contained two or three thin capillary setæ. This circumstance is easily verified in such species as I have examined, and it leads me to suggest that we are in error in regarding these structures as tentacles. They are much more probably the reduced and modified notopodia of the peristomial segment itself.

It may be of some advantage to dwell on this point at greater length. In Annelids the *peristomium* is the segment behind the prostomium, and it can be generally recognised and homologised throughout the group. This fact is, however, due more to its position than to any morphological characters which distinguish it from those succeeding, and it is generally recognised as the most anterior of the trunk-segments, which has been considerably modified in connection with the mouth. With regard to its identity with the other segments of the trunk, Goodrich says :— "Careful modern researches (Vejdovsky, Wilson, etc.) have shown that in Oligochætes the peristomium exhibits the essential characters of a true segment. It develops as a region surrounding the mouth, in which are formed a pair of mesoblastic somites which become hollowed out to form the cœlom; a ganglionic thickening is produced ventrally, which soon fuses with that of the succeeding segment; a nephridium (head kidney) is developed. In the Polychætes—in some cases, at all events,—it has been shown that a pair of somites are formed in the peristomium, become hollowed out, and even give rise to peritoneal funnels. Nephridia are almost invariably developed in this segment. In Polychætes, moreover, a pair of lateral appendages are often developed, though they generally become highly modified. In fact, it becomes evident, when we examine the development and the adult structure of the peristomium in the various groups of the Annelids, that it is really a metamere strictly comparable to the posterior segments, even when much modified owing to its position at the anterior end of the animal."

In the Syllids, the Polynoids, and other groups, the peristomium consists of a segment which bears on each side a dorsal and a ventral cirrus. That these are the remains of a typical parapodium, in which the notopodium and neuropodium with their setæ have disappeared, is shown by a number of cases amongst the Polynoids, which could probably be duplicated in other families, where the first segment carries not only cirri but also setæ. In *Polynoë extenuata*, described by Claparède, the peristomium shows an aciculum and a couple of setæ. In *Pontogenia*, *Sthenelais*, *Sigalion*, and in *Palmyra* amongst the Palmyridæ, the peristomium possesses a notopodium with several setæ, and only differs from the succeeding segments in the absence of neuropodial setæ.

These cases show that the peristomium may be an almost

unmodified trunk-segment. On the other hand, it often occurs that trunk-segments fuse with the peristomium and then lose their parapodia, with the exception of the dorsal and ventral cirri. So that the same process which has affected the peristomium may modify the succeeding segments in a similar way.

The object of this digression is to show that the retention of a parapodium in the peristomium of *Phyllochætopterus* is by no means without parallel in other families of Polychæts. The constancy of the phenomenon makes it of generic value, and suggests that possibly the rudimentary notopodium has undergone a change of function which we cannot yet appreciate.

Description of a new Species, *P. anglica*, from British Waters, and a Comparison of those Species of the Genus which form True Colonies.

Phyllochætopterus anglica. (Pl. VI.; Text-figs. 9, 10, 12.)

Phyllochætopterus *of moderate size* (2–12 *cm. in length*), *with eye-spots. Anterior region with a variable number of segments* (13–16); *a single enlarged seta in each parapodium of the 4th segment. Median region also with a variable number of segments* (11–25). *Tubes creeping; often several run parallel to each other, with short lateral connections. More than one individual in the same system of tubes.*

Locality. English Channel.

I obtained this species in March of the present year (1913), while working at the laboratory of the Marine Biological Association at Plymouth. Tubs of *Chætopterus*-tubes were brought in from trawlers, apparently obtained from an area a little south of the Eddystone. Attached to the *Chætopterus*-tubes were numbers of other very slender tubes, often arranged in parallel bundles. Sometimes they were embedded in the substance of the larger tube, at other times they were entirely surrounded by large colonies of *Alcyonium*, so that it seems that the communities of *Phyllochætopterus anglica* are of comparatively long standing.

In the character of its colonies this species seems to be intermediate between *P. socialis* and *P. prolifica*, and it will be profitable to make a definite comparison :—

(1) In *P. prolifica* (Pl. IV.) the colony is usually contained in a single, long, stolon-like tube (sometimes bifurcating) with a number of very short branches communicating with the exterior, and consists of a comparatively large number of small individuals which reproduce asexually with rapidity (at least in the summer).

(2) In *P. socialis* the colony seems to occupy a large number of parallel and adherent tubes, the communication between which can only be made out with great difficulty. In each mass of tubes the individuals are, however, of the same sex. A single tube contains two or three individuals.

(3) In *P. anglica* (Pl. VI. figs. 15, 16) the colony is likewise contained in a number of tubes, which tend to run parallel, but are not, as a rule, adherent. The open nature of the colony leaves

no but doubt that the tubes are connected. Usually each constituent tube contains a single individual longer than those of *P. prolifica*. Small subsidiary apertures may be placed at the end of branchlets of the main tube, as in *P. prolifica*.

These distinctions which I have attempted to draw may, on further examination of the genus, prove to be insufficiently grounded. I feel quite certain, however, that *P. prolifica* in the N.E. Pacific does not usually form the dense colonies characteristic of *P. socialis*, nor do connected tubes run parallel as in *P. anglica*.

It is possible, too, that these three species differ in the extent to which asexual reproduction is developed in each. In particular, it may be mentioned that *P. prolifica* is the only species in which asexual reproduction was found to be proceeding at the moment of discovery.* In *P. anglica* I was not successful in finding any example which showed signs of recent regeneration. It is probable that this phenomen takes place later in the year than the time when my specimens were collected, but I incline to believe that autotomy and regeneration are never so frequent as in *P. prolifica*, a circumstance which accounts for the smaller number of individuals contained in much longer tubes.

In the morphological characters of the animals themselves, I must confess to a considerable difficulty in distinguishing between these three species. Mr. Crossland has pointed out that some species of *Phyllochætopterus* are easily recognised by definite characters, like the number of modified setæ in the notopodium of the fourth setigerous segment, the presence or absence of eye-spots, and the number of setæ in the notopodium of the posterior region (C), as well as the character of the tubes. In all four species, which have developed asexual reproduction, eye-spots are present, a single strengthened seta is usually found in the notopodium of the fourth segment and a single seta in each notopodium of region C, while the tubes they inhabit are creeping and branched. It seems to me that there is sufficient difference between the forms here described to preserve them as distinct species, though they must, from their morphological characters, as well as from their manner of life and reproduction, be classed as very nearly related. There are, moreover, differences in the size, the number of segments in the several regions of the body, and in the shape of the prostomium and peristomium which help to supplement the biological peculiarities which I have indicated above.

Comparison of the external Morphology of those Species of Phyllochætopterus *which form True Colonies.*

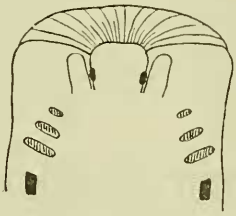
(1) *The Prostomium and Peristomium.*—In *P. anglica*, the prostomium (text-fig. 9) is rather broad, though small, and its borders are marked by a line of dark pigment. The eyes are placed on the extreme side of the head, and are overlapped and

* This was in the summer (May–July).

hidden by the peristomial appendages, which are here small and slender objects. The peristomium forms a well-developed funnel. In *P. prolifica*, on the other hand, though I have examined a large number of individuals, I have experienced considerable difficulty in making out the relations of the pro- and peristomium. I think it is possible to say that the prostomium is smaller, and less definite than in *P. anglica*, and that the peristomial appendages are quite minute, and do not cover the eyes. The peristomial funnel is complete.

I have been able to examine two of the species described by Mr. Crossland, and preserved in the Museum of Zoology at Cambridge, to test the variation which occurs in the different species of *Phyllochætopterus*. In *P. elioti* from Zanzibar the peristomial appendages are comparatively large and definite structures, though they do not cover the eyes, the prostomium is much better developed than in *P. anglica* and *P prolifica*, but the peristomial funnel completes little more than a semicircle (Crossland, 2, pl. xiv. fig. 1).

Text-figure 9.



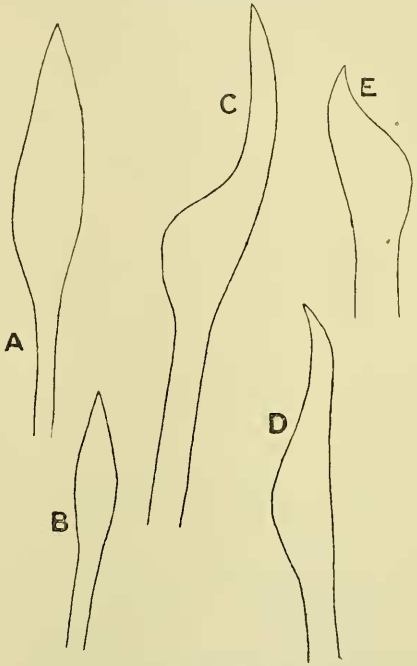
Phyllochætopterus anglica.
Dorsal view of head and anterior segments.

In *P. pictus*, also from the neighbourhood of Zanzibar, the prostomium is rather large and fleshy, and the peristomium does not form a funnel but a conical elevation, divided behind by a median groove; the mouth is a small slit-like aperture. In another species *P. aciculigerus* described by Crossland, the peristomium is very much reduced, forming a cone with a rounded mouth. The prostomium is small, but definite.

From the small series of species here examined, I have ventured to draw some conclusions. The prostomium is always a very definite organ, except in a species like *P. prolifica*, where the peristomial collar is quite complete. The peristomium, however, varies a good deal. In *P. pictus* and *aciculigerus* it is small and rudimentary, while in other forms it is developed into a funnel—markedly incomplete, for instance, in *P. elioti*, less so in *P. anglica*. With the completion of the peristomial funnel in *Mesochætopterus taylori* and *Chætopterus* we have the suppression of the prostomium and the complete disappearance of the peristomial appendages. I think that the conical peristomium is primitive and that the formation of the peristomial funnel is a direct adaptation to microphagous habits.

(2) *The Setæ.*—A good deal of time has been spent in endeavouring to fix the value of the notopodial setæ of the anterior region as a basis of classification. It must, however, be stated that the results of this enquiry are entirely negative. The variation in the shape of the setæ is almost endless, and seems to occur indiscriminately in species and individual. The dorsalmost setæ in each parapodium are nearly always lanceolate and symmetrical. Individual variations occur even here in the

Text-figure 10.



Phyllochætopterus anglica.
Series of notopodial setæ from anterior region.

length and thickness of the head, and substantial modification in the more ventral setæ. The following rough classification of types of modification may be given as indicating the range of variation :—

I. Shortening of the head, which remains symmetrical (text-fig. 10, A, B).

II. An increasing asymmetry of the head.

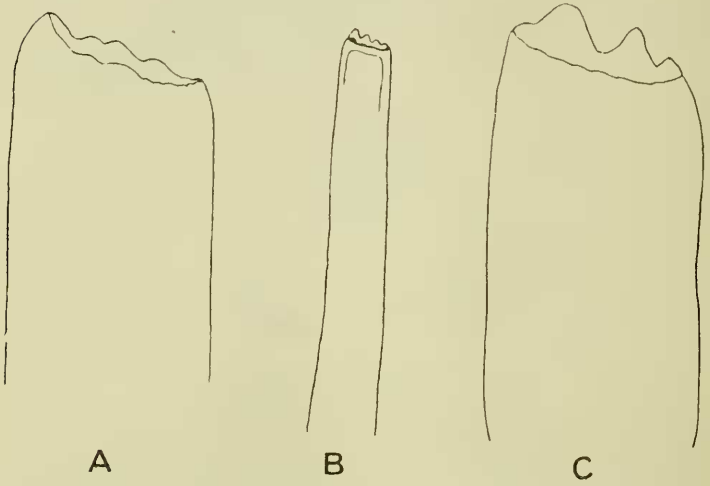
(*a*) The head remains long and is drawn out into a long asymmetrical tip (text-fig. 10, C, D).

(*b*) The head is much shortened, with a short tip and a broad edge (text-fig. 10, E).

Minor variations are found, according to whether the sides of the head are curved or straight, to the degree of attenuation and curvature of the tip.

In none of the species which have been described hitherto has a full examination of the notopodial setæ been made. Such figures and notes as are given are of little value, then, in fixing the species; but they show, I think, that the same variations which occur in *P. prolifica* and *anglica* occur in all. I have been able to compare these with the actual specimens of *P. claparedei*, *pictus*, and *elioti* described by Crossland, and this examination supports my conclusion that the notopodial setæ are too variable to base specific characters upon.

Text-figure 11.



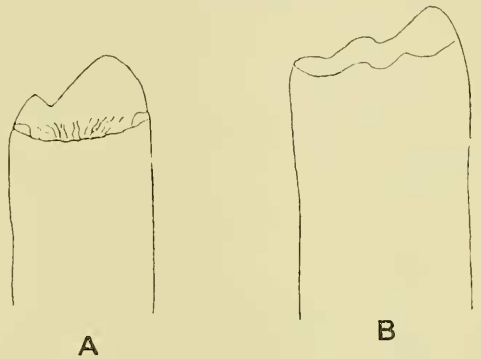
Phyllo chætopterus prolifica. Enlarged setæ from 4th segment.

The specially modified setæ in the fourth segment are always figured in descriptions of species, and their configuration is sometimes considered to be of diagnostic value. There is, without doubt, a recognisable type for each genus of the Chætopterids, but the modifications of this are so many, varying even in the same individual, that I find it impossible to regard the shape of the seta as in any way a specific feature. In all species of *Phyllochætopterus*, the seta appears to end in a blunt elliptical crown. One or both of the sides of this are raised into a cuspate ridge, one ridge being generally higher than the other. The number of cusps is highly variable, and so is their development. Thus in *P. prolifica* (text-fig. 11, A, B) there are on the highest side 3, 4, or 5 cusps, and generally the cusps have a fairly equal development. In some cases, however, like text-fig. 11, C, one or

more of the cusps are of greatly increased size. The lower side of the crown is usually smooth or slightly crenulated.

In *P. anglica* the setæ are often very similar to those of *P. prolifica*. Two setæ are here figured to show the extent of the variation in number and size of cusps. In one of them (text-fig. 12, A) there are only two cusps, one of which is very large. In the other (text-fig. 12, B) the appearance of a cuspate lower border will be noticed.

Text-figure 12.



Phyllochætopterus anglica.

Enlarged setæ from 4th segment of two individuals.

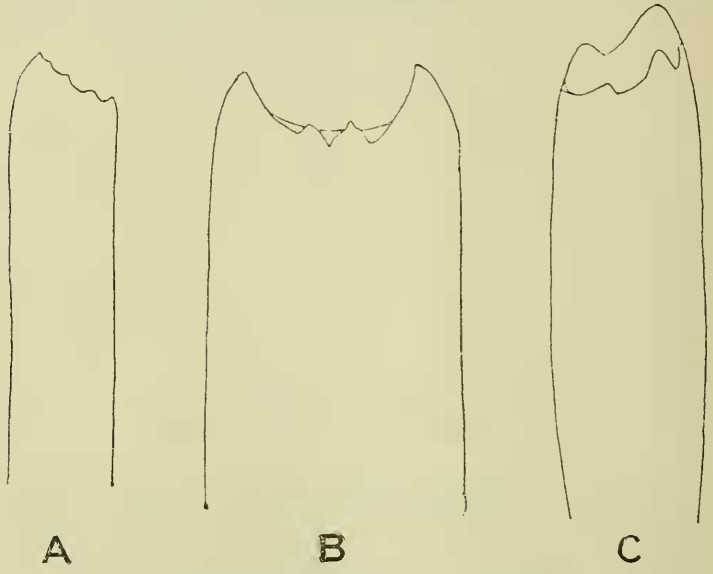
The figure which Crossland has given of *P. pictus* shows an enlarged seta of a type different from any which I have described for *P. prolifica* and *anglica*. In text-fig. 13, C, however, I have drawn another seta from the 4th parapodium of a *P. pictus* collected by Crossland, and I think, it will be seen to be easily derived from the seta shown in text-fig. 12, A (*P. anglica*). The cusps on the lower border are better developed in the first, but otherwise the two are strongly similar. The bulging shaft of the seta mentioned by Crossland is shown also in my mounted specimen, but I have observed similar phenomena in *P. prolifica*.

P. elioti is another species which from the published description appears to have a very definite type of strengthened seta. I mounted two or three setæ from Crossland's specimen, and one of these (text-fig. 13, B) agreed fairly well with his figure. On the upper side the two external cusps are greatly enlarged, contrasting with the two small intermediate cusps (not seen at all in Crossland's figure). But another seta (text-fig. 13, A) showed an oblique crown with small equal cusps, like the usual type of *P. prolifica* etc.

It is very probable that the average seta of a species is different

from that of another species, but the point I wish to emphasise is that the setæ of the fourth parapodium vary greatly, and a statement as to their character can only be made after examination of a large series of individuals. It has been shown in the preceding part of this section that the other setæ of the anterior region are always variable, and it would have been rather surprising if those modified setæ which are found in the fourth parapodium had been found to belong to types fixed for each species.

Text-figure 13.



A. B. *Phyllochætopterus elioti*. C. *P. pictus*.

Enlarged setæ from 4th segment.

Some Remarks on the Genera *Spiochætopterus* and *Phyllochætopterus*.

Until 1856 *Chætopterus* was the only member of the family known, but in that year Michael Sars (**10** *a*) described the genus *Spiochætopterus* to include a species (*S. typica*) from Norwegian waters, which differed from *Chætopterus* in possessing long peristomial tentacles. In 1863, Grube (**7**) instituted a third genus, *Phyllochætopterus*, for a worm from the Adriatic. But the two forms are undoubtedly similar, and de Quatrefages, in his 'Histoire des Annélés,' goes so far as to include Grube's polychæt, *P. gracilis*, in the earlier genus *Spiochætopterus*.

Spiochætopterus typica was described as living in a jointed transparent tube. It has long peristomial tentacles, but a pair of

peristomial appendages was not observed. There are three well-differentiated regions, the median of which contains two segments with bifid foliaceous notopodia, exactly like those described in all species of *Phyllochætopterus*. There is only one strongly modified seta in the 4th segment. In the posterior region there is a bundle of fine setæ in the notopodium, but the neuropodium is stated to be without uncini.

Phyllochætopterus gracilis, as originally described by Grube, possesses a pair of short peristomial tentacles. It is possible that in the cases examined the greater part had been broken off, but Grube thinks this was unlikely. Or they may really be very long peristomial appendages, the tentacles being entirely lost. The observations are quite inadequate on this important point.

The 4th segment of the anterior region appears to have more than one strengthened seta on each side, though the number is not actually given. There are two segments here also in the median region, and they are similar in form to those of *Spiochætopterus*. The posterior region contains segments, the notopodia of which each contains more than one seta; but Grube expresses himself as uncertain whether the neuropodium contains uncini or not.

Neither of these forms has ever been rediscovered so far as I know, and so these descriptions remain still inadequate and uncorrected. But as they stand, I share the opinion of de Quatrefages concerning them, that no sufficient cause is shown for placing the Adriatic form in a separate genus. The differences of the tentacles might be explained as errors of description, and the variation of number of strengthened setæ in the 4th segment is unimportant. The presence or absence of uncini in the neuropodium of the posterior segments is a moot point in both, but it is probably their extremely small size which enabled them to escape detection.

The next question which arises is whether these two forms are similar to those better-known species which are grouped to-day under the genus *Phyllochætopterus*. For that genus is characterised by the possession of a pair of peristomial appendages, as well as the long tentacles, and they may possibly have been overlooked by Sars and Grube in their respective discoveries. The numbers of enlarged setæ in the 4th segment and in the notopodium of the posterior segments and that of the segments in the median region are not definite generic characters. The structure of the segments of the median region of these two forms is identical with the type usually associated with *Phyllochætopterus*. It is however, I think, a matter of some importance that these two early forms should be rediscovered and their position more accurately defined. For the present, the generic name *Phyllochætopterus* must certainly be retained, and I trust it will not be necessary to go back to the older genus *Spiochætopterus*. But in the table of the Chætopterids which is given by Crossland he includes *Spiochætopterus* as distinct from *Phyllochætopterus* through

its single pair of tentacles. I should like to point out that both genera were originally described as possessing only a single pair of peristomial processes, and that we are not in a position to correct the description of the type-species.

Literature.

(1) Claparède, Edouard.—Les Annélides Chétopodes du Golfe de Naples. Seconde Partie. (Pp. 76–94 for Chætopterids.)

(2) Crossland, Cyril.—On the Marine Fauna of Zanzibar and British East Africa, from Collections made by Cyril Crossland in the Years 1901 and 1902.—Polychæta. Part I. Proc. Zool. Soc. London, 1903, vol. i. pp. 169–176.

(3) Crossland, Cyril.—The Polychæta of the Maldive Archipelago, from the Collections made by J. Stanley Gardiner in 1899. Proc. Zool. Soc. London, 1904, vol. i. pp. 270–286. pls. xviii., xix. (For *Phyllochætopterus aciculigerus* and *gardineri*.)

(4) Enders, Howard.—A Study of the Life-History and Habits of *Chætopterus variopedatus* Renier et Claparède. Journ. Morph. Philadelphia, vol. xx. 1909, pp. 479–531, pls. i.–iii

(5) Gravier, C.—Annélides Polychètes de la Mer Rouge. Nouv. Arch. Mus. d'Hist. Nat. sér. 4, t. viii. 1906. (For *Telepsavus bonhourei*. see p. 191, pl. iii. figs. 209–213.)

(6) Gravier, C.—Sur la régénération des extrémités du corps chez le Chétoptère et chez la Marphyse sanguine. Bull. Mus. Paris, 1909, pp. 14–17; Ann. Sci. Nat. (Zool.) Paris, sér. 9, t. ix. 1909, pp. 129–155.

(7) Grube, E.—Beschreibung neuer oder wenig bekannter Anneliden. Arch. f. Naturgeschichte, 1863, p. 52.

(8) Ivanow, P.—Die Regeneration des vorderen und des hinteren Körperendes bei *Spirographis spallanzanii* Viv. Zeitschr. f. wiss. Zool. Bd. xci, pp. 511–558, Taf. 20–22.

(9) Laffuie, J. Joyeux-.—Étude Monographique du Chétoptère. Arch. Zool. Exp. Gén. sér. 2, t. viii. 1890, pp. 245–360, pls. xvi.–xx.

(10) Langerhans, P.—Ueber einige canarische Anneliden. Nova Acta Leop. Car. Akad. Naturf. Bd. xlii. Nr. 3, 1881. (For *Phyllochætopterus gracilis*.)

(10 *a*) Sars, M.—Fauna littoralis Norvegiæ, ii. 1856.

(11) Vaney, C. et Conte, A.—Recherches expérimentales sur la régénération chez *Spirographis spallanzanii* (Viviani). C. R. Soc. Biol. 1899, p. 973.

(12) Watson, A. T.—A Case of Regeneration in Polychæt Worms. Proc. Roy. Soc. ser. B, vol. lxxvii. 1906. pp. 332–6.